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DISCUSSION AND CORRESPONDENCE OPINIONS ON SOME CILIARY ACTIVITIES

IN SCIENCE for August 4, 1916, Professor C. Grave has questioned the accuracy of some of my conclusions concerning the ciliary mechanisms of lamellibranchs, dealing with the ingestion of food, that were published in the *Journal of Morphology*, Vol. 26, No. 4.

Those statements of mine which he has difficulty in accepting are:

1. Volume alone determines whether the collected foreign matter that reaches the palps shall proceed to the mouth or shall be sent from the body on outgoing tracts of cilia.

2. A lamellibranch is able to feed only when waters are comparatively clear—when diatoms are brought to the gill surfaces a few at a time. In muddy waters all suspended particles, of whatever nature, are led to outgoing tracts.

3. There is no selection or separation of food organisms from other water-borne particles.

4. The direction of the beat of cilia is never changed.

The only facts bearing on these statements, that are offered from Professor Grave's own experience, are those derived from an oyster-feeding experiment made at Buzzards Bay, and these bear only on the second statement, namely, that lamellibranchs feed only when waters are comparatively free from suspended particles.

Professor Grave has referred fully enough for the purpose, to the litigation that led to his experiment. Planted oysters had died in great numbers at the mouth of the Monument River after dredging operations were begun in the oyster field, and below it in Buzzards Bay. He wished to show that oysters could live in the turbid water. Taking individuals gathered at a distance, he deprived them of food for three days, then at a certain point immersed them "in the turbid water" for periods of one, two and three hours, at the end of which periods their stomachs contained from 2,850 to 18,500 food particles. In some cases, also, there was so much sediment that a diatom count was not possible. Some oysters were allowed to remain on the bottom for two

weeks, and "all thrived and made perceptible growth of shell."

My contention, based on thousands of examinations of the operation of the palps in very many species of lamellibranchs, and extending through many years, was that when solid particles in sufficient volume are brought to the apposed palp surfaces, they overflow the narrow tracts leading to the mouth from either side, so as to touch outgoing tracts that border them, and by these are carried away and eventually removed from the body. My assumption was that, in this particular case, waters had, during long intervals, been so laden with fine sand and bast fibers from decaying vegetable matter, liberated by the dredging operations, that oysters over the field in general had been, through the action of the ciliary mechanisms of the palps, so often deprived of nourishment that they were gradually weakened and finally destroyed. They were not killed at once, for during a part of the ebb tide relatively clear water coming down from flats above the bay presented conditions favorable for feeding. Some had remained alive for more than two years under the adverse conditions. Here and there even the young had grown for a time. The condition of the field in 1911 indicated, and the owners of the beds testified, that, in general, there had been a gradual elimination.

The results of Professor Grave's feeding experiment seems to him to "show conclusively that oysters can and did feed actively in waters that were turbid with sediment, a fact that is in direct opposition to Dr. Kellogg's conclusion numbered (2) in this paper [and in the present one], and one that casts doubt upon the correctness of the three other conclusions herein discussed."

During a period of two weeks, Professor Grave's oysters "thrived and made perceptible growth of shell." This is not a very full or definite statement of his net results in the matter of growth, but it is all that he has given. At the same time, it was the testimony of all the oyster planters, as well as my own, after I had examined their beds, that, far from thriving, a large proportion of their planted oysters had died, after several months—so

many that the oystermen had almost entirely abandoned the field, and sought other occupation. This fact was completely established. Professor Grave admits an "unusually large" death rate, adding that the "planters readily imagined that the poor condition and death of their oysters were in some way causally connected with this sediment in the water." Commissioners, then referees, and finally a jury, readily imagined the same thing, and awarded them damages for their losses. Why should Professor Grave's oysters have thrived while those of the oystermen died?

It is not without interest that the death of the planted oysters, and other lamellibranchs on the same ground, could not be accounted for by the presence of starfish, drills or other enemies, or from any disease. On the other hand, Professor Grave's oysters may have survived for two weeks, and added a "perceptible growth" to the shell for several possible reasons.

A few of the bed oysters had lived, not two weeks, but two years or more after dredging had begun. A good many survivors were found behind a bar that deflected one of the two main flood currents away from them. The accident of position may have been favorable to Professor Grave's oysters, but they would have lived much longer than two weeks anywhere on the beds.

During the summer of 1911, when this experiment was made, dredging was intermittent. Frequently so little of it was being done that the flood tides bore comparatively little sediment over the beds.

Again, at the time of this experiment most of the dredging was being done at a much greater distance from the beds than formerly, and the water was proved to bear very much less silt than in 1909 and 1910 when the mortality on the beds had been greatest. This fact alone should be sufficient to explain Professor Grave's result.

That oysters in good condition, "gathered from a bed far removed from the scene of the dredging operations," should fail in two weeks to become emaciated—or should thrive—was to be expected. Nor, considering

the possible conditions, was I surprised at Professor Grave's results in his examination of the contents of their stomachs. I was not able to see that the fact that his oysters fed "in waters that were turbid with sediment" was at all in opposition to my conclusion. "Turbid with sediment" is a relative—a very indefinite—term. I believe that any lamellibranch is able to take into its stomach any suspended particles, sand grains as well as diatoms, even in turbid water, until a definite point is reached at which they become too numerous, and that then they are all carried out of the body. It is unfortunate that in my work on the ciliary mechanisms I have not determined precisely how turbid the water must be, that is, how large a proportion of suspended matter must be present, to bring the discharging mechanism into action; but in my experiments there was always such a point. Professor Grave asserts his disbelief even in the existence of a normal mechanism of this kind as I have described it, though I have no reason to think that he ever took the trouble to look for it. I am not particularly anxious over final judgment on that matter, or on the "Kellogg theory" of its operation.

The most interesting of Professor Grave's assumptions, however, concern food selection, and my statement that the beat of cilia is nowhere reversed. He contends that cilia of "certain tracts" of the palps are capable of being reversed, as in the case of the oyster, "resulting perhaps from their stimulation directly or indirectly by food particles," and that this "may be the mechanism by which the selection is effected."

One is a little puzzled to understand, from the statement of it, what is the mechanism and its operation according to the Grave theory. Does the reversal of cilia from stimulation by food particles cause the rejection of food particles? If so, to what purpose? Or does stimulation by *food* cause the rejection of *sand*, and not of food particles? That would be interesting. Professor Grave's theory credits the oyster with the possession of a delicate sense of taste, and he is rather scornful because mine does not. Does the taste of sand,

like the taste of crab juice in the case of *Metridium* mentioned by Professor Grave, cause its acceptance, or perhaps its rejection? He says only that food particles, and not that sand or other matter in suspension, cause the reversal that results somehow in the selection of something, either food or material not useful as food, it is difficult to determine which. I judge that some diatoms are rejected, and that other diatoms, and sand, are selected. *Rhizosolenia*, "abundant in salt water, are seldom found in the digestive tract of the oyster." They are not excluded on account of their spiny structure, we are told, because their size is not sufficiently great to prevent their being carried by cilia currents or entering the mouth. Has Professor Grave made observations to determine whether their spiny structure or size is great enough to cause their rejection by the outgoing tracts that, up to this time, I had supposed I had seen in a very great many instances? I must say that I have not, myself, in the case of this particular diatom; but I have seen certain other diatoms excluded, though not in the oyster.

And according to this view, it seems necessary to assume that sand is selected and sent into the mouth, for Professor Grave tells us that it is a "fact that the stomach contents of oysters always contain a larger volume of sand than of food organisms." I am grateful to him for adding that this is difficult to explain on the Kellogg theory. I am sure that he will not contend that everywhere, where oysters and other lamellibranchs "thrive," suspended sand is in greater volume than suspended diatoms. When it is not, do oysters select sand, and reject diatoms that are suitable for food? They must do the one thing or the other, or both, if sand is always to be more abundant than diatoms in their stomachs. It is difficult to understand how statements of this sort can so easily and confidently be made, and this one indicates how limited have been Professor Grave's studies on the stomach contents of oysters, to say nothing of those of other lamellibranchs. My own study of this subject has not been extensive, either, but I have material on hand to disprove this state-

ment, if it is applied to the group of lamellibranchs in general. My "theory," that has been attacked, does not apply to the oyster alone, but to all lamellibranchs, most of which demonstrate it more clearly than the oyster does.

What may be called the argument of Professor Grave concerning the supposed reversal of the cilia beat on the palp tracts, with results that he makes no pretence of having observed, and has not formulated in his own mind, is based on the statement of Engelmann that he has actually witnessed this reversal on the palps of lamellibranchs, and on the facts that a reversal occurs in *Stentor* and other protozoa, and in *Metridium*, resulting in the selection of food and in the rejection of other particles.

I do not feel that I am in a position to object that even one who has never studied the matter himself should, without any question or hesitation, accept the statement of Engelmann and reject my own, on the matter of cilia reversal on the lamellibranch palp. "Why then," asks Professor Grave, after quoting Engelmann, "if a reversal of cilia and selection of food takes place in lamellibranchs, did Dr. Kellogg fail to see the reversal process?" The matter is settled at once; but I venture to suggest that somebody else should examine the palps of *Schizotherus*, of some species of *Cardium*, and of some other lamellibranchs in which the palp folds are large, to see what he can find. Let him be warned that he has no simple task, to be decided by a few observations. The turmoil on the palp face is so extraordinarily confusing that it seems just possible that even Engelmann may have been mistaken. I have supposed that I also have seen a reversal of the cilia beat on the palp, but many years ago concluded that I was mistaken. It is entirely possible that my present belief is erroneous, but I would prefer to be corrected by some one who has at least made an effort to study a few lamellibranchs, instead of studying papers. That protozoa reverse the cilia beat adaptively in food selection is suggestive in this case; but protozoa are not lamellibranchs, and I had hoped that the argument from analogy had been aban-

doned by biologists, especially in cases in which there was no possible excuse for it.

Professor Grave has fortified himself against confirmation of my views by assuming the position that even if no reversal of the beat of cilia is to be observed when my methods are employed, "it seems clear that it was due to the fact that the animals on which he made his observations were, in every case, in a mutilated condition." I removed the shell, "and," he says, "in its removal the adductor muscle was cut and the visceral ganglion, which is imbedded in this muscle, was necessarily severely injured. Under such a condition of shock normal behavior is not to be expected, especially in the case of activities that may be subject to nervous control."

Here is another pure assumption, made without observation, or even the opinion of some one else to substantiate it. I have no reason to believe that there is any element of truth in it; and I have several reasons for believing that it is not true that cilia of the palp, gill or mantle tracts are in any way under the control of the nervous system (such as the continued and unchanged beat on fragments of any of these organs, and also on isolated single cells, facts that can not be presented here).

Now the action of gill and mantle cilia are precisely the same in normal and in "mutilated" *Pectens*, and in some other lamellibranchs that open the shell valves widely, a condition that I have observed very many times. Why should Professor Grave not naturally expect these cilia tracts, as well as those of the palps, to behave abnormally from the detachment of the end of the adductor muscle? For he must know that gills and mantle receive large nerve trunks from the visceral ganglion, while the palps do not. The palps are so situated that they can not be examined without removing the shell valve, or using great force to pry the valves far apart by stretching the adductor muscles, and I have not seen their currents otherwise. I would like to ask Professor Grave if Engelmann was careful not to mutilate the lamellibranch on the palp of which he discovered a reversal of the cilia beat?

Finally, the cause of my mistakes in observation, we are told, was that when the end of the adductor muscle was separated from its shell attachment, the visceral ganglion "was necessarily injured." I venture to offer the information that, when one actually tries the experiment, it will be found that a shell valve may quite easily be removed from any lamellibranch without touching the visceral ganglion, or any of the nerves arising from it; and that to say that it is necessarily injured in the process is but to add another to the list of these entirely unsupported assumptions. This *a priori* method of arriving at truth ought to be even more out of place in present-day biology than the employment of analogies. Very likely, the use of the binocular dissecting microscope, which I did not have because it was not yet invented, will show that I made mistakes; but years were spent in making the observations before they were published, and perhaps I may be pardoned for objecting to their summary dismissal, in some cases with a very small show of reason, and in others with none at all.

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CHLOROSIS OF PINEAPPLES INDUCED BY MANGANESE AND CARBONATE OF LIME

It has been recently found by M. O. Johnson at the Hawaiian Experiment Station that the chlorosis of pineapples occurring on highly manganiferous soils can be cured by spraying the leaves with ferrous sulphate.¹ As the chlorosis of pineapples growing on strongly calcareous soils in Porto Rico can also be cured by the application of iron salts, some have the idea that the two forms of chlorosis are the same. Although the phenomena are remarkably similar in many respects, and although the cure is the same, it is not yet clear that they are identical. It seems advisable to point out certain differences that seem to exist in the two kinds of chlorosis.

¹ *The Pacific Commercial Advertiser*, Honolulu, Hawaii, July 21, 1916, and a personal communication.